AN INTRODUCTION TO TERRETRIAL ECOLOGICAL STOICHIOMETRY

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Ecological stoichiometry

The imbalance between elemental abundance and energy in an ecosystem affects organism evolution and interactions with other organisms (Sterner and Elser 2002). The relative abundances, or stoichiometry, of nutrients in an ecosystem puts constraints on organismal life history traits that change in time and are selected for by the environment. Any particular organism must take from the environment the nutrients needed for survival and reproduction and expel the rest. The study of the ways in which organisms meet these demands and how they compensate for imbalances between elemental demand of tissue composition and intake of nutrients is called ecological stoichiometry (ES; Hessen et al. 2013). In general, the nutritional needs determined by the elemental content of an organism are not in equilibrium with the food it eats. The imbalances between these nutrient demands of producers and consumers influence pools and fluxes of the elements within an ecosystem, which affects life-history traits, metabolism, and fitness of the organisms in the food web (Sterner and Elser 2002). By determining the variability of nutrients in space and time by measuring carbon, nitrogen and phosphorus ratios (C:N:P) in organisms, a better understanding of ecosystem dynamics, organismal physiology, and biogeochemistry can be reached.

ES was used initially as a framework to connect the relative abundance of elements in an ecosystem and the effects this has on organisms in that ecosystem (Olff et al. 2009). Historically, the first application of ES came from Alfred Redfield who described the ratio of C:N:P in deep, oceanic phytoplankton to be 106:16:1 and constant throughout the biosphere (Cleveland and Liptzin 2007). Continued research into ES built validity in many different fields such as ecology, biochemistry, evolution,

and global nutrient cycling. Contemporarily, it seeks to connect the intrinsic elemental dependency of biological systems to ecosystem function and food web interactions (Martinson et al. 2008). Ultimately, three questions should be answered through ES: how do elemental imbalances arise in an ecosystem? How do these imbalances affect organismal evolution? And what does this do to the pools and fluxes of elements in an environment? First, important elements need to be identified.

Ecologists studying ES have tended to focus on nitrogen (N), carbon (C), and phosphorous (P) as these elements are imperative in many cellular function like protein synthesis and cellular respiration, and present in many macromolecules necessary to sustain life (Vrede et al. 2004). Nitrogen for instance is prevalent in proteins and nucleic acids, whereas P is found in nucleotides and ribosomal RNA (rRNA; Sterner and Elser 2002). Thus, the Growth Rate Hypothesis (GRH) states that organisms with increased growth rate will require more P (lower C:P ratio) relative to an organism with a slower growth rate because P is needed for rRNA production (Main et al. 1997; Matzek and Vitousek 2009). This is critical for protein synthesis, the mechanism by which growth occurs. Nitrogen and P availability also limit sexual signaling in many insect species such as crickets and grasshoppers (Orthopterans; Bertram et al. 2006), drive varying productivity in plants such as *Eucalyptus grandis* and *Avicennia marina* (Conroy et al. 1992; Naidoo 2009), cause shifts in food selection (Harrison et al. 2014), and affect microbial growth and decomposition rates of detritus (Enríquez et al. 1993). Analyzing varying N:P ratios in organismal excreta and tissue composition has been historically useful in determining elemental fluxes and the nutrient dynamics and availability in ecosystems (Sterner and Elser 2002).

Ecologists build food webs and mass balances to approximate the exchange of energy and elements through trophic interactions. ES seeks to determine and evaluate the exchange of mass and energy in a system through the imbalance of elemental ratios between food web interactions. The imbalance between elemental content of food and organismal demand influences growth rate of an organism, allocation of time and resources, and reproductive success. However, the mechanisms by which these imbalances affect ecosystems are not known.

Terrestrial Ecosystems

Ecological stoichiometry has historically focused on aquatic ecosystems due to differences in aquatic and terrestrial ecosystems. In aquatic ecosystems, unicellular primary producers dominate where in terrestrial ecosystems, multicellular primary producers dominate (Bartels et al. 2012). When introducing terrestrial ES, we will focus of leaves and grass as they are the majority of biomass turnovers in many terrestrial ecosystems (Aerts and Chapin 2000).

Leave and grass are the primary component of elemental production in many terrestrial ecosystems and are the main source of biomass turnover per year (Aerts and Chapin 2000). Also, in terrestrial grazing ecosystems, leaves and grass are common components of availability of C, N and P for the primary consumers. The base of the food web and the related C, N and P of the primary producers determine the available nutrients and energy to the rest of the terrestrial food web (Polis and Strong et al. 1996). From a logical standpoint, fats, carbohydrates, and proteins are made mainly of these molecules. The law of the minimum states that the limiting element available to an organism determines the growth rate of that organism (Lieth 1973; Danger et al. 2008).

Therefore, a limiting element in a terrestrial environment, available elements should explain aspects of organismal development and nutrient transfer, which cascadingly affects other pools and fluxes of such elements in the ecosystem. To introduce the study of ES from a terrestrial aspect, the elemental composition and stoichiometry of the producers, consumers and their nutrient demand is the first step.

Terrestrial producer/consumer stoichiometry

On land, plants dominate most of the biomass in terrestrial environments, especially in temperate and tropical climates (Woodwell and Whittaker 1968). Plants tend to have relatively plastic C:N:P ratios due to their sessile nature, geochemically variant substrates, and biochemically variant cellular structures (Güsewell 2004). As C tends to not be limited because of the CO_2 in the atmosphere and the photosynthetic nature of autotrophs, we will focus mainly on N and P. Plant growth rates in terrestrial ecosystems can be limited by both N and P availability, which ever one is in less supply obeying von Liebig's law of the minimum. Soil age is imperative in determining the availability of P in terrestrial systems because P is increasingly sequestered due to mineralization on time scales of 10^3 - 10^5 years (Walker and Syers 1976; Vitousek 2004). Because both N and P are both in the soil, the roots are closer to the limiting nutrient supply and can grow more rapidly relative to above-ground tissue (stems and leaves; Chapin 1980). The growth rate of the roots is constrained by the rate of carbohydrates supplied by the stems; this rate of carbohydrates supplied by to roots is itself a function of leaf growth rate, C fixation and N availability, where the root:shoot ratio is determined by light:nutrient balance in optimizing the overall growth (Rastetter and Shaver 1992). As stated, C fixation is not limited by C availability, and therefore the

rate of carbohydrate production is only limited by the relative abundances of needed N and P.

With enrichment techniques, we can experimentally manipulate the effects of added N and P to terrestrial environments to determine ecological changes due to limited elemental availability. Elser and colleagues (2007) enriched N and P separately in freshwater and terrestrial ecosystems and found that they had equal effects in both, suggesting that N and P are necessary for all photoautotrophs (increasing N alone increases N:P, while increasing P decreases N:P). Increasing N and P had synergistic effects in biomass in all ecosystems: marine, terrestrial and freshwater (Ågren et al. 2012). It is important to note that this study only looks at autotrophs only, not the entire food chain. However other studies show that P is the more limiting terrestrial environments because anthropogenic N has been input over the past decades leading to higher N:P (Güsewell 2004).

Broad models of terrestrial organismal growth rate in response to nutrient limitation were proposed independently by Ågren and Droop through the productivity equation and Droop equation (Droop 1983; Ågren 1988). Both models gives similar results over a wide range of taxa-dependent growth rate responses to specific nutrient limitation. That is, over many autotroph species, the reduction of a limiting nutrient will have a proportional reduction in growth rate in a similar pattern from trees to photosynthetic algae. The growth of biomass in autotrophs is usually C-dependent in an environment and is usually not limiting; the C:limiting nutrient content is used to determine the growth of autotrophs, especially in terrestrial environment, which produces the relative abundances of nutrients for all other consumers in an ecosystem.

With the assumption of the GRH and C dependency to growth rate, mechanistic models like the productivity equation for autotrophs can approximate growth rate variation of species in different environments on the relative proportion of autotroph biomass and limiting nutrient content.

The particular ratios of C:P and C:N of terrestrial autotrophs generally are much larger relative to freshwater and oceanic ecosystems (Sterner and Elser 2002). For example, foliar C:P ranges from 115 up to 5990 with a mean C:P of 970, which is very high in C abundance. Likewise, leaf C:N ranges from 7.5 to 225 with a mean C:N of 36, relatively variant high to other ecosystems. However, the distinguishing characteristics of terrestrial ecosystems that impact the C:N:P ratios and nutrient abundances should be noted. Terrestrial ecosystems have site-dependent variation in resource and element availability, thus influencing the C:N:P of an organism. As mentioned earlier, mobile animals have the ability to change substrates not applicable to sessile plants like terrestrial autotrophs. Aquatic autotrophs can rely of currents and water movement to disperse variable nutrient content, while soil N:P is static in a particular environment. Lastly, the C:N:P of tissue composition in terrestrial organisms changes between species, as with any ecosystem. The causes of such contrasting variability in terrestrial nutrient composition is important for any terrestrial ecologist who seeks to investigate energy flow, nutrient cycling and food-web dynamics.

Though specific regulatory processes that mediate and govern terrestrial autotroph C:N:P are not known, influential variables and hypothetical models supported by evidence have been proposed. For example, Tilman (1988) and Chapin (1993) emphasized the functional morphology of terrestrial plant tissue and the opposing

demands that occur on vertical gradients between light and nutrients. Implicit is trade-off between allocating resources in downward root growth for nutrient acquisition and upward shoot growth for light acquisition. As stated prior, this trade-off in resource allocation establishes a root:shoot ratio corresponding with a autotroph nutrient state. Utilizing this, a light:nutrient ratio can be generated from the nutrient availability in an environment and species-dependent root:shoot ratio, establishing a wide range of nutrient demands in terrestrial plants (Aerts and Chapin 2000). As this relationship has been supported by contemporary research, more nuanced proposals have been devised to explain the pattern. Hobbie and colleagues (1993) used the functional gradient of light and the trade-off of resources to hypothesize the nutrient ratios of plants under different conditions. Under high fertility (high nutrient availability), the acquisition of light will become limited due to self-shadowing, displaying an inverse relationship of light and nutrients across terrestrial communities, generally corresponding to large deciduous growth. In highly fertile ecosystems, C:N will be low in plant tissue. While in low nutrient and high light environments, slow-growing herbs and bryophytes with have low tissue turnover rates, corresponding to high C:N. This pattern shows the clear function of C:N:P stoichiometry with evolutionary morphology, functionality, and physiological traits. Following from this, the C:N:P influence on terrestrial autotrophs and their ecological dynamics should directly and indirectly affect all other levels of consumers and in the ecosystem.

Insects are of the most diverse and abundant taxa on Earth and their ecological role has become clear in many studies, whether that be pollination or nutrient decomposition (Humphrey et al. 1999). Because insects comprise a large amount of

terrestrial primary consumers, their body C:N, N:P and C:P ratios are important in understanding terrestrial ecological stoichiometry holistically. Bertram et al. (2008) showed that terrestrial insects are mainly limited by P. Likewise, data collection of different herbivorous insect stoichiometry has enable researchers to quantify mean values (Villar-Argaiz et al. 2000). For terrestrial herbivorous insects, the mean C:N is 6.5, the mean C:P is 116, and the mean N:P is 26.4 with coefficients of variation 0.29, 0.62 and 0.38, respectively (Elser et al. 2000). As much of the focus in the field of ES has emphasized aquatic environments, the current pursuit of terrestrial stoichiometric data is imperative in understanding and elucidating the role of elemental composition of specific species in nutrient cycling.

The C:N:P ratios of herbivorous insects show high variation in elemental composition even in closely related species, while distantly related species may converge to similar C:N:P ratios (Bertram et al. 2008). Therefore, the predictability of C:N:P in the environment and the impact of animals like insects is not particularly clear; however, allocation of resources into development of phenotypic traits and tissue types is a driving factor. Nitrogen and P have been linked in the processes of growth, development, reproduction and nutrient/energy allocation because of their biochemically content in proteins, ATP, and many other cellular components. In the search for causal implications of nutrient availability in ecosystems, P variability seems to be of particular importance and has led to the formulation of the Growth Rate Hypothesis, developed by Sterner and Elser (2002), which states that P is the limiting nutrient and the rate determining factor for the growth rate of organisms because of the biochemical function, i.e. protein synthesis, of the macromolecules (rRNA) in which P resides. Sterner and

Elser propose that a fundamental and necessary amount of P is needed because P-rich RNA, in particular rRNA, is essential in the growth of an organism, and therefore P availability relative to organismal P demand should determine the growth rate of the organism. Supporting this hypothesis, studies have shown strong relationships (slope close to 1) between the organismal % P body composition and organismal % RNA across many taxa (Dobberfuhl 1999). The relationship between primary consumers like herbivorous insects and their nutrient demands with terrestrial autotroph producers like plants and their C:N:P composition becomes clear in terms of the GRH. The P composition in terrestrial autotrophs directly affects the growth rate of herbivores as P availability in a system with sufficient C and N is the limiting nutrient. With this in mind, interactions between autotroph C:N:P stoichiometry and consumer nutrient demand and acquisition go far beyond the influences between insects and plants. Therefore, the GRH connects the trophic interactions throughout all levels of a food web with the biochemical demands of organismal C:N:P stoichiometry, which provides a framework for life-history trait evolution, ecosystem energy budgeting and dynamics, and nutrient cycling.

Terrestrial ES is trying to determine a connection between organism variation in C:N:P and ecosystem function. The plant-herbivore interaction has established a fundamental in driving consumer resources and is impacted by C:N:P composition. This interaction can be modified in two ways: changing the consumer nutrient demands (elemental body composition) and changing the resource stoichiometry (González et al. 2011). Returning to herbivorous insects as an example, a comprehensive overview of N and P variation in terrestrial insects in relation with elemental abundance in the

environment is present from various studies (Fagan et al. 2002). Nitrogen was widely the limiting nutrient across herbivorous insects and N and P varied greatly interspecifically and intraspecifically, showing counter evidence that N is fundamental in determining growth in insect-plant interactions, not P. Continued research by Markow et al. (1999) showed high variation in drosophila N and P content, correlating with resource content. Thus, evidence exists supporting both claims that N and P are limiting nutrients for herbivore insects. What is not controversial is that availability of N, P and overall C:N:P tissue composition in terrestrial plant tissue profoundly affects herbivore growth rate, which influences the dynamics of entire ecosystems.

Wood makes up a large portion of the biomass of autotrophs. The C:nutrient ratio content of wood is relatively high because of the large amount of carbonaceous structural material in plants. Once the tree dies, the C-rich wood must be broken down for the nutrients and energy to be acquired by other species or returned to the ecosystem. Though high C content gives wood the rigidity and strength useful to humans, most species could not survive off only wood because of the large imbalance between plant C:nutrient and consumer C:nutrient stoichiometry (Haack and Slansky 1987). However, it is common knowledge that termites eat wood. Termites have a C:N ratio between 4 – 12 (Matsumoto 1976), while wood can have a C:N in excess of 1000 (Higashi and Abe 1997). So how do termites compensate for this large variation between consumer nutrient requirement and food? Due to the large amounts of C in wood, the excess C must be excreted; concomitantly, a high proportion of N from the wood must be conserved. A common method among termite species in retaining N is a symbiotic relationship with N-fixing gut bacteria (Täyasu et al. 1994). The fixed N is

absorbed and metabolized into uric acid where it then is excreted into the hindgut. Here, other symbionts further convert uric acid to ammonia and amino acids, which are available for reabsorption, conserving as much N as possible (Potrikus and Breznak 1981). Also uric acid is energetically expensive, and this may be useful in using excess C. Other ways to release C is through methane production via methanogenic gut bacteria (Prestwich and Bentley 1981). Symbiotic relationships with fungi help to modify the feces of termites to extinguish excess C as CO^2 so the available feces can be eaten is more nutrient-dense (Higashi and Abe 1997). Lastly in times of N shortage, termites will simply transition to cannibalism as this obviously increases N uptake relative to wood. The clear balancing act between retaining limiting nutrients and releasing excess C in the attempt to even out the imbalanced between food and tissue stoichiometry is imperative for all organisms, not just termites.

Summary

Ecological stoichiometry is a framework through which scientists seek to describe the energy flow and nutrient transfer of environmental carbon, nitrogen, phosphorous and other important elements through a food web. The idea that organisms need to find an elemental balance between their tissue and food has long been known; however, how this drives evolution of organisms in an ecosystem in unknown. Through the application of using ES on terrestrial environments, we may soon understand how and why a particular nutrient change will comprehensively affect ecosystems.

References

1. Ågren, G. I., Wetterstedt, J. Å., & Billberger, M. F. (2012). Nutrient limitation on terrestrial plant growth–modeling the interaction between nitrogen and phosphorus. *New Phytologist*, *194*, 953-960.

2. Aerts, R., & Chapin III, F. S. (2000). The mineral nutrition of wild plants revisited: A re-evaluation of processes and patterns. *Advances in Ecological Research, 30*, 1-67.

3. Bartels, P., Cucherousset, J., Steger, K., Eklöv, P., Tranvik, L. J., & Hillebrand, H. (2012). Reciprocal subsidies between freshwater and terrestrial ecosystems structure consumer resource dynamics. *Ecology, 93*, 1173-118

4. Bertram, S. M., Schade, J. D., & Elser, J. J. (2006). Signalling and phosphorus: correlations between mate signalling effort and body elemental composition in crickets. *Animal Behaviour*, *72*, 899-907.

5. Bertram, S. M., Bowen, M., Kyle, M., & Schade, J. D. (2008). Extensive natural intraspecific variation in stoichiometric (C: N: P) composition in two terrestrial insect species. *Journal of Insect Science*, *8*, 1-7.

6. Chapin III, F. S. (1980). The mineral nutrition of wild plants. *Annual review of ecology and systematics, 11*, 233-260.

7. Chapin III, F. S. (1993). Functional role of growth forms in ecosystem and global processes. *In Scaling physiological processes*, 287-312.

8. Cleveland, C. C., & Liptzin, D. (2007). C: N: P stoichiometry in soil: is there a “Redfield ratio” for the microbial biomass?. *Biogeochemistry, 85*, 235-252.

9. Conroy, J. P., Milham, P. J., & Barlow, E. W. R. (1992). Effect of nitrogen and phosphorus availability on the growth response of *Eucalyptus grandis* to high CO2. *Plant, Cell & Environment*, *15*, 843-847.

10. Danger, M., Daufresne, T., Lucas, F., Pissard, S., & Lacroix, G. (2008). Does Liebig's law of the minimum scale up from species to communities?. *Oikos, 117*, 1741-1751.

11. Dobberfuhl, D. R. (1999). Elemental stoichiometry in crustacean zooplankton: Phylogenetic patterns, physiological mechanisms, and ecological consequences. PhD Dissertation, Arizona State University, Tempe, AZ.

12. Droop, M. R. (1983). 25 years of algal growth kinetics a personal view. *Botanica marina*, *26*, 99-112.

13. Elser, J. J., & Urabe, J. (1999). The stoichiometry of consumer-driven nutrient recycling: Theory, observations, and consequences. *Ecology*, *80*, 735-751.

14. Elser, J. J., Fagan, W. F., Denno, R. F., Dobberfuhl, D. R., Folarin, A., Huberty, A., & Siemann, E. H. (2000). Nutritional constraints in terrestrial and freshwater food webs. *Nature, 408*, 578.

15. Elser, J. J., Acharya, K., Kyle, M., Cotner, J., Makino, W., Markow, T., & Hood, J. A. (2003). Growth rate–stoichiometry couplings in diverse biota. *Ecology Letters*, *6*, 936-943.

16. Enríquez, S. C. M. D., Duarte, C. M., & Sand-Jensen, K. A. J. (1993). Patterns in decomposition rates among photosynthetic organisms: the importance of detritus C: N: P content. *Oecologia*, *94*, 457-471.

17. Fagan, W. F., Siemann, E., Mitter, C., Denno, R. F., Huberty, A. F., Woods, H. A., & Elser, J. J. (2002). Nitrogen in insects: implications for trophic complexity and species diversification. *The American Naturalist*, *160*, 784-802.

18. González, A. L., Fariña, J. M., Kay, A. D., Pinto, R., & Marquet, P. A. (2011). Exploring patterns and mechanisms of interspecific and intraspecific variation in body elemental composition of desert consumers. *Oikos, 120*, 1247-1255.

19. Güsewell, S. (2004). N: P ratios in terrestrial plants: variation and functional significance. *New phytologist*, *164*, 243-266.

20. Haack, R. A., & Slansky, F. JR., (1987). Nutritional ecology of wood-feeding Coleoptera, Lepidoptera, and Hymenoptera. *Insect Adaptations to Woody Environments, 15,* 449-486.

21. Harrison, S. J., Raubenheimer, D., Simpson, S. J., Godin, J. G. J., & Bertram, S. M. (2014). Towards a synthesis of frameworks in nutritional ecology: interacting effects of protein, carbohydrate and phosphorus on field cricket fitness. *Proceedings of the Royal Society of London B: Biological Sciences*, *281*, 20140539.

22. Hessen, D. O., Elser, J. J., Sterner, R. W., & Urabe, J. (2013). Ecological stoichiometry: an elementary approach using basic principles. *Limnology and Oceanography, 58*, 2219-2236.

23. Higashi, M., & Abe, T. (1997). Global diversification of termites driven by the evolution of symbiosis and sociality. *Biodiversity, 115,* 83-112.

24. Hobbie, S.E., Jensen, D.B., & Chapin, F.S., III. (1993). Resource supply and disturbance as controls over present and future plant diversity. E*cosystem Function of Biodiversity, 30,* 385-407.

25. Humphrey, J. W., Hawes, C., Peace, A. J., Ferris-Kaan, R., & Jukes, M. R. (1999). Relationships between insect diversity and habitat characteristics in plantation forests. *Forest ecology and management*, *113*, 11-21.

26. Lieth, H. (1973). Primary production: terrestrial ecosystems. *Human ecology, 1,* 303-332.

27. Main, T. M., Dobberfuhl, D. A., & Elser, J. J. (1997). N: P stoichiometry and ontogeny of crustacean zooplankton: a test of the growth rate hypothesis. *Limnology and Oceanography*, *42*, 1474-1478.

28. Markow, T. A., Raphael, B., Dobberfuhl, D., Breitmeyer, C. M., Elser, J. J., & Pfeiler, E. (1999). Elemental stoichiometry of Drosophila and their hosts. *Functional Ecology, 13*, 78-84.

29. Martinson, H. M., K. Schneider, J. Gilbert, J. Hines, P. A. Hambäck, & W. F. Fagan. (2008). Detritivory: Stoichiometry of a neglected trophic level. *Ecological Research*, 23, 487-491

30. Matsumoto, T. (1976). The role of termites in an equatorial rain forest ecosystem of West Malaysia. I. Population density, biomass, carbon, nitrogen and calorific content and respiration rate. *Oecologia, 22*, 153-178.

31. Matzek, V., & Vitousek, P. M. (2009). N: P stoichiometry and protein: RNA ratios in vascular plants: an evaluation of the growth-rate hypothesis. *Ecology Letters*, *12*, 765-771.

32. Naidoo, G. (2009). Differential effects of nitrogen and phosphorus enrichment on growth of dwarf Avicennia marina mangroves. *Aquatic Botany*, *90*, 184-190.

33. Olff, H., Alonso, D., Berg, M. P., Eriksson, B. K., Loreau, M., Piersma, T., & Rooney, N. (2009). Parallel ecological networks in ecosystems. *Philosophical Transactions of the Royal Society, 364*, 1755-1779.

34. Polis, G. A., & Strong, D. R. (1996). Food web complexity and community dynamics. *The American Naturalist*, *147*, 813-846.

35. Potrikus, C. J., & Breznak, J. A. (1981). Gut bacteria recycle uric acid nitrogen in termites: a strategy for nutrient conservation. *Proceedings of the National Academy of Sciences, 78,* 4601-4605.

36. Prestwich, G. D., & Bentley, B. L. (1981). Nitrogen fixation by intact colonies of the termite *Nasutitermes corniger*. *Oecologia*, *49*, 249-251.

37. Rastetter, E. B., & Shaver, G. R. (1992). A model of multiple-element limitation for acclimating vegetation. *Ecology, 73*, 1157-1174.

38. Sperfeld, E., Halvorson, H. M., Malishev, M., Clissold, F. J., & Wagner, N. D. (2016). Woodstoich III: Integrating tools of nutritional geometry and ecological stoichiometry to advance nutrient budgeting and the prediction of consumer-driven nutrient recycling. *Oikos*, *125*, 1539-1553.

39. Sterner, R. W., & Elser, J. J. (2002). *Ecological stoichiometry: the biology of elements from molecules to the biosphere*. Princeton, NY: Princeton University Press.

40. Täyasu, I., Sugimoto, A., Wada, E., & Abe, T. (1994). Xylophagous termites depending on atmospheric nitrogen. *Naturwissenschaften, 81*, 229-231.

41. Tilman, D. (1988). *Plant strategies and the dynamics and structure of plant communities*. Princeton, NY: Princeton University Press.

42. Villar-Argaiz, M., Sánchez, J. M., Cruz-Pizarro, L., & Carrillo, P. (2000). Life history implications of calanoid *Mixodiaptomus laciniatus* in C: N: P stoichiometry. *Verhandlungen, 27*, 527-531.

43. Vitousek, P. M. (2004). *Nutrient cycling and limitation: Hawai'i as a model system.* Princeton, NY: Princeton University Press.

44. Vrede, T., Dobberfuhl, D. R., Kooijman, S. A. L. M., & Elser, J. J. (2004). Fundamental connections among organism C: N: P stoichiometry, macromolecular composition, and growth. *Ecology*, *85*, 1217-1229.

45. Walker, T. W., & Syers, J. K. (1976). The fate of phosphorus during pedogenesis. *Geoderma, 15*, 1-19.

46. West, G. B., Brown, J. H., & Enquist, B. J. (1997). A general model for the origin of allometric scaling laws in biology. *Science, 276*, 122-126.

47. Woodwell, G. M., & Whittaker, R. H. (1968). Primary production in terrestrial ecosystems. *American Zoologist*, *8*, 19-30.